



Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada

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Abstract

We examined the spatial patterns of 297 human-caused grizzly bear mortalities from 1971 to 2002 within the Central Rockies ecosystem (CRE) of Canada to explore relationships between mortalities and variables reflecting human development, terrain, and vegetation. Using logistic regression, we modelled the distribution of grizzly bear mortalities based on local landscape attributes as well as examining variation among demographic status, seasons, and mortality type. Grizzly bear mortalities were concentrated in three main regions of the CRE: (1) Lake Louise; (2) Banff town site; and (3) Alberta Provincial lands near the Red Deer River. We found no evidence for environmental differences in mortality locations between sexes or season, while sub-adult male and legal harvest mortalities were more dispersed than other mortalities. Models describing the relative risk of mortality were positively associated with human access, water, and edge features, while negatively associated with terrain ruggedness and greenness indices. Model predictions fit well with independent data. Overall, relatively little of the landscape was secure from human-caused mortality for grizzly bears. This would be most directly remedied by controlling access.

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1. Introduction

Large carnivores are particularly vulnerable to extinction because of their low density, high trophic level, and low reproductive rates (Russell et al., 1998; Purvis et al., 2000a,b). Anglo-European settlement of previously ‘unoccupied’ lands together with increasing human density have been well correlated with historic carnivore extirpations (Woodroffe, 2000; Mattson and Merrill, 2002). Currently, however, effective land-management policies can be important determinants

of population persistence (Channell and Lomolino, 2000; Linnell et al., 2001; Homewood et al., 2001). For North American grizzly bears, *Ursus arctos*, populations and distributions have been substantially reduced in the past century (Mattson and Merrill, 2002). Much of this loss has occurred in the contiguous United States and southern Canada (McLellan, 1998) and can be explained by historic conflicts between humans and bears reflecting pioneering attitudes and corresponding to two of Diamond’s (1989) evil quartets of extinction: overkill and habitat destruction/fragmentation.

Much research on grizzly bear conservation has focused on habitat selection and the spatial distribution of grizzly bear habitats using radiotelemetry data

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(e.g., Mace et al., 1996, 1999; Waller and Mace, 1997; Nielsen et al., 2002). Common factors used to describe bear occurrence include landcover or vegetation type (Mace et al., 1996; McLellan and Hovey, 2001), distance to streams and forest edge (Nielsen et al., 2002; Theberge, 2002) vegetation indices from satellite data, such as greenness (Mace et al., 1999; Stevens, 2002), and terrain ruggedness (Theberge, 2002; Naves et al., 2003). Although substantial information on the spatial occurrence of bears exists, relatively little has been done to examine how spatial factors, especially human-related features, influence human-caused grizzly bear mortality in local populations (see however, Johnson et al., in press; Mattson and Merrill, in press). It is well accepted that survival, particularly of adult females, is the most important factor shaping population growth and long-term viability of grizzly bear populations (Wiegand et al., 1998; Pease and Mattson, 1999; Boyce et al., 2001; McLoughlin et al., 2003). Given the threatened status and/or nature of many remaining grizzly bear populations, including those in the Central Rockies ecosystem (CRE, McLellan, 1998), the identification of mortality sinks (Knight et al., 1988) is crucial to the future conservation of grizzly bears. Mortality risk maps may be useful for describing habitat-based population viability (Boyce, 2002) or the identification of bear habitats and core areas with high conservation value based on multidimensional habitat models of survival and reproduction (Naves et al., 2003). Although methods are well developed for survival modelling (Cox and Oakes, 1984), most areas of current grizzly bear range lack the required information on individual exposure and death. Alternative approaches that make use of ad hoc government mortality records are required. Development of regional spatial mortality risk models for grizzly bears would be an important contribution to conservation.

Grizzly bear populations within Canada, although not as reduced as within the contiguous United States, still face substantial pressures from habitat degradation and reduced population growth rates caused from excessive mortality (McLoughlin et al., 2003). Currently, only 37% of the 3.5-million-km² grizzly bear range is considered secure, with the remaining 63% considered vulnerable (Banci et al., 1994). Risks associated with these vulnerable populations are the expansion and development of resource extraction activities, including oil and gas exploration and development, timber harvesting, and mining. Previous research on human-caused grizzly bear mortality has shown a strong relationship between bear mortalities and roads (McLellan, 1989). As resource extraction activities enter an area, initially without much access, road construction provides entry for hunters, poachers, and settlers, the major cause of grizzly bear mortality

(McLellan, 1989). Even in 'pristine' landscapes such as national parks where grizzly bears are protected from hunting, as much as 100% of known adult grizzly bear mortalities occurred within 500 m of roads or 200 m of high use trails (Benn and Herrero, 2002). Likewise, examinations of survival and mortality in the Greater Yellowstone ecosystem revealed the highest risk of mortality for grizzly bears in areas of high road density and for those animals experiencing repeated management actions (Boyce et al., 2001; Johnson et al., in press). Most often, researchers have focused on habitat selection and assumed that the identification of areas most frequently occupied by animals represent high quality habitat or contribute to fitness (Garshelis, 2000). In certain circumstances, however, areas frequented by animals and therefore identified as 'high' quality habitat within habitat models, can be considered attractive sinks where risk of mortality is high (Delibes et al., 2001; Naves et al., 2003). Identifying attractive sinks as high quality habitat would be misleading for management and conservation action. Research that identifies mortality sinks, or the opposite secure high-quality sites, as it relates to human features, terrain, and vegetation, is important if our goal is to maintain viable future populations of grizzly bears.

In this paper, we develop predictive models and maps that describe the distribution of human-caused grizzly bear mortalities for the Alberta and Yoho National Park portions of the CRE of southern Canada. Our goal was to understand, through modelling, the relationships among bear mortality locations and landscape-level physiographic and human variables. More specifically, we were interested in: (1) examining the spatial density of grizzly bear mortalities; (2) evaluating possible differences in the physiographic attributes of mortality locations relative to demographic status, season, and mortality type; and (3) developing predictive models that estimate the relative probabilities of bear mortality (risk) given multi-variable combinations of physiographic variables. Our working hypothesis is that grizzly bear mortalities are related to factors describing human accessible habitats in those locations where bears are likely to frequent. Mattson et al. (1996a,b) conceptualizes this as the frequency of contact between bears and humans. At increasingly larger spatial and temporal scales, however, the lethality of contact can differ based on jurisdictional boundaries and temporal changes in management regime (Mattson et al., 1996a,b; Mattson and Merrill, 2002). We attempt to examine spatial expressions of these concepts in the CRE of Canada using empirical modelling of grizzly bear mortality locations, animal use locations, and geographic information system (GIS) data typical of most grizzly bear habitat models.

2. Study area

This study encompassed a 29,264-km² area of the CRE in southern Alberta and a small portion of adjacent British Columbia, Canada (Fig. 1). This study area encompasses a portion of the known distribution of grizzly bears in western Canada. This area included Banff and Yoho National Parks and an Alberta Provincial area south of Banff referred to as Kananaskis Country. The area was bordered to the west by the Continental Divide and Yoho National Park, being no further than 117.0°W longitude. The northern boundary was primarily along Highway 11 and occurred south of 52.5°N latitude. The southern border was at latitude 50.0°N, while the east border was irregular in shape, but no further east than 114.0°W longitude. Legal harvest of grizzly bears, through a limited entry spring hunt since 1988, occurred in the areas outside of Banff and Yoho National Parks and Kananaskis Country (Fig. 1). Mountainous terrain dominated the study area with elevations varying from 839 m along the North Saskatchewan River at Rocky Mountain House to 3588 m along the Continental Divide. Given a strong gradient in elevation, a diverse array of local ecosystems and plant communities existed, but most generally could be di-

vided into the following five ecoregions: (1) alpine; (2) sub-alpine; (3) upper boreal-cordilleran; (4) aspen parkland; and (5) montane.

3. Methods

3.1. Mortality location data

We collected grizzly bear mortality information across the CRE for a 32-year period from 1971 to 2002. Mortalities were defined as both dead bears and those bears translocated a sufficient distance to be considered eliminated from the population. For each mortality record, the location (UTM coordinates), accuracy of location, month, year, sex, age, and cause of mortality were obtained from National Park and Provincial management records (Benn, 1998; Benn and Herrero, 2002). However, because locations of mortalities in Alberta were provided at the scale of the township, and some mortalities in the National Parks were imprecise or missing, persons involved with the mortality event were interviewed to associate specific coordinates on a map and locations were then digitised into a GIS. Accuracy for each observation was categorized from accurate (<100 m) and reasonable (within a stated distance to a known road, trail, or drainage development), to an estimate or unknown accuracy. For spatial mortality models, we used 279 accurate and reasonably accurate locations that were associated with human-caused events (e.g., we removed the relatively few natural mortality events and those with inaccurate assignments). Bear mortalities from human causes were classified into two classes: (1) legal harvest; and (2) non-harvest/other (self-defense, First Nation, accidents, railroads, highway, problem wildlife, research, and translocation).

3.2. GIS (spatial) predictor variables

We generated seven geographical information system (GIS) layers that were related to land cover, terrain, and humans. Land cover was estimated from Landsat TM satellite imagery dated from 1995 to 1998 and occurring at a 30-m pixel resolution. Land cover was initially classified into nine classes: conifer forest, deciduous forest, shrub, avalanche, grass, cropland, ice/snow, rock/bare soil, and water (Wierzchowski, 2000). Based on ground truth locations, the overall accuracy of this map was 76% with a kappa index of agreement at 0.712 (J. Theberge and S. Jevons, unpublished data). This map was further simplified by reclassifying the image into five more general land cover categories, since a number of classes were rare and/or ecologically similar for our purposes. These reclassified categories were conifer forest, deciduous forest, shrub (shrub and avalanche), grassland (grass and cropland), and non-vegetated areas

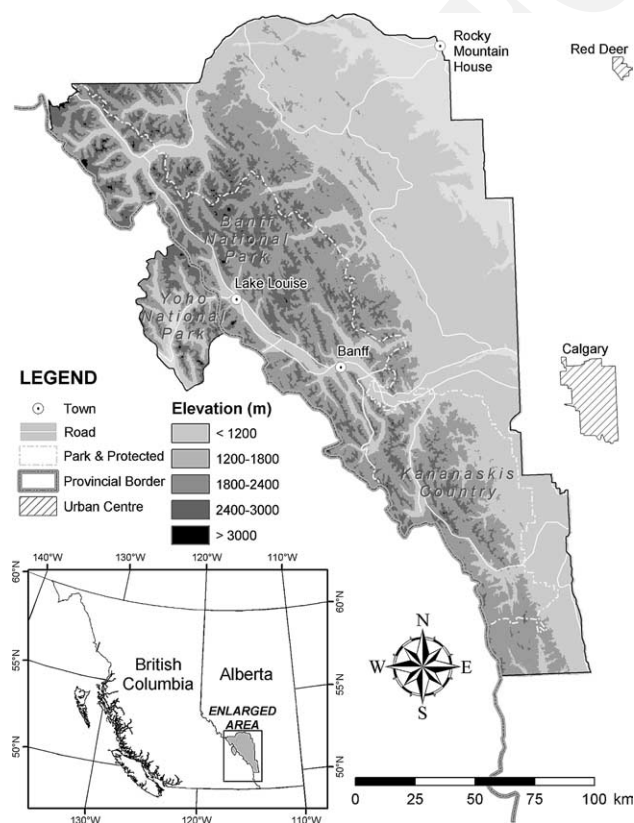


Fig. 1. Study area map depicting elevation, study area boundary, Province border, places, and general location within Alberta and British Columbia, Canada (small inset map in upper left corner).

(ice/snow, rock/bare soil, and water). Under this classification, there was an overall accuracy of 81%. From the classified land cover imagery, we further derived a grid (30-m pixel) representing the distance (km) to edge of any nearest land cover.

Using the same satellite imagery, we derived a greenness index based on a tasselled-cap transformation of the Landsat TM bands (Crist and Cicone, 1984), which has been found to relate to leaf area index (LAI) and vegetation productivity (White et al., 1997; Waring and Running, 1998). Greenness has previously proven useful for identifying grizzly bear use in mountainous regions (Manley et al., 1992; Mace et al., 1996, 1999; Gibeau et al., 2002; Nielsen et al., 2002; Stevens, 2002), and as such has been recognized as a surrogate of grizzly bear habitat quality (Stevens, 2002).

Using hydrographic GIS data, we also derived a 30-m grid that represented the distance (km) to any nearest water feature (water body, permanent stream, intermittent stream, indefinite stream). As a final distance metric, we calculated, again in a 30-m grid, the distance (km) to nearest linear human use feature (motorized or non-motorized), but did not include exploratory seismic lines that are common to areas outside of the Parks. To characterize terrain, we generated a terrain ruggedness index (TRI) within 300-m circular moving windows, as previous examinations have found this scale to be an important predictor of bear occurrence (Theberge, 2002). The equation for TRI, modified from that of Nellemann and Cameron (1996) and calculated in a GIS with a 30-m DEM, was as follows:

$$\text{TRI} = \frac{(\text{aspect variation} \times \text{average slope}) / (\text{aspect variation} + \text{average slope})}{100}, \quad (1)$$

where aspect variation was measured in a 300-m circular window surrounding each pixel and calculated following the relative richness index of Turner (1989) as the proportion of total number of aspect classes in the moving window over the maximum number of aspect classes in the study area. Slope average was calculated for each pixel based on the average of slopes for all pixels within 300-m circular windows. Excluding TRI and distance to water, the remaining GIS predictor variables were temporally relevant to only the most recent mortality events. We thus make the assumption that the majority of features were established near to or before 30-years ago. We examined potential collinearity between the above linear predictors by using Pearson correlations and variance inflation factors (VIF). Collinearity was assumed if correlations were $>|0.6|$ or the VIF scores were much greater than one (Chatterjee et al., 2000). Given these examinations, we excluded elevation derived from a DEM for all models because it was corre-

lated with both TRI ($r = 0.73$) and greenness ($r = -0.62$) and the VIF was much greater than 1 (VIF = 2.99).

3.3. Data analysis

3.3.1. Spatial densities of grizzly bear mortalities

To qualitatively examine spatial patterns and concentrations of grizzly bear mortalities, we used three separately scaled moving windows to calculate the total density of mortality locations in a GIS. These moving window analyses corresponded to a scale of (1) 520-km² (12,869-m radius) or the estimated average multi-annual 95% fixed kernel home range for female grizzly bears in the CRE (Stevens, 2002); (2) 900-km² (16,929-m radius) or the approximated lifetime home range of a female grizzly bear in Yellowstone (Blanchard and Knight, 1991); and (3) 1405-km² (21,153-m radius) or the estimated average multi-annual 95% fixed kernel home range for male grizzly bears in the CRE (Stevens, 2002). The 900-km² scale was used by Mattson and Merrill (2002) for examinations of grizzly bear extirpations in the contiguous United States, and could be considered a conservative estimate for the CRE since our home range estimates were not lifetime estimates. All human-caused mortalities over the past 32 years were summed within moving windows and applied to 100-m pixels (1-ha grid) in a GIS map. Because mortality locations existed beyond the extent of the study area boundary, where GIS information was unavailable, we felt comfortable that potential edge biases in moving window density esti-

mates were minimized. All pixels with a mortality density of 0 were qualitatively considered secure sites, while those exceeding 31 mortalities (≥ 1 mortality/yr) were qualitatively considered high mortality zones. We summed all secure and high mortality pixels to assess the total proportion of the study area that could be considered in either state over the past 32 years, while further assessing the proportion of secure areas in non-vegetated areas; considered non-habitat a priori. We do not address temporal changes in mortality because Benn (1998) and Benn and Herrero (2002) previously examined this issue

3.3.2. Mortality differences among demographic status, season, and mortality type

We used logistic regression to assess relationships between landscape attributes of mortality locations (GIS predictor variables) and the categories of demographic status, season, and mortality type (response variables).

Of the documented grizzly bear mortalities, information regarding the sex and age of the animals was known for 244 and 254 locations respectively, while age and sex data were known for 232 observations. To examine potential differences in mortalities relating to demographic status, we evaluated either sex or sex-age class composition. Sex was contrasted for either female (1) or male (0) observations, while for sex-age class composition, we tested for sub-adult (3–5-yr-old) males mortalities (1) versus all the other (0) mortalities (e.g., young, adult, and sub-adult females). We selected sub-adult males for our comparison, because previous research has shown that differences in mortality rates exist for this group, but not for others (McLellan et al., 1999). To examine whether seasonal differences were present, we compared mortalities that occurred during the berry season (1) with those mortalities that occurred outside of the berry season (0). We defined the berry season to be the period from 1 August to 31 October. During this time, grizzly bears in the region forage on Canada buffaloberry *Shepherdia canadensis* and numerous species of blueberry and huckleberry *Vaccinium* spp. (Hamer and Herrero, 1987; Hamer et al., 1991; Nielsen et al., 2003). Finally, we examined whether environmental differences existed in mortalities associated with legal harvest locations (1) compared to other human-caused mortalities (0). However, because all legal harvests (legal hunting mortalities) occurred outside of protected National parks (e.g., Banff and Yoho) and Kananaskis Country, we excluded these protected areas from this analysis. All mortality locations with attribute data identifying sex, sex-age class, legal harvest, and season were used for model fitting.

For each comparison, logistic regression was used to contrast each category or class (response variable) against the six uncorrelated environmental habitat, terrain, and human-related GIS variables hypothesized to influence bear mortality. Because the land cover variable was categorical, we used an indicator contrast with conifer forest as our reference cover type. Model significance was assessed using a likelihood ratio χ^2 test, while coefficient significance was based on a Wald χ^2 test. If model or coefficient significance was lacking, we interpreted such results to mean that tested demographic, season, or mortality categories were not useful for understanding the spatial distribution of grizzly bear mortalities, at least for those GIS environmental data tested. For significant demographic status, season, or mortality type classes, specific mortality distribution models were developed as described below.

3.3.3. Random versus mortality locations – mortality distribution models

To characterize the landscape within the defined study area, we generated a sample of random (2-dimensional uniform distribution) locations with a sam-

pling intensity of 1 point per 5-km² ($n = 5852$). These random landscape locations (0) were contrasted with human-caused, mortality locations (1) using an availability-presence design with the following log-linear form:

$$w(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_k x_k), \quad (2)$$

where $w(\mathbf{x})$ represents the relative mortality distribution function (low to high mortality rank) and β_i the mortality coefficient estimated from environmental predictors x_i (Manly et al., 1993). Coefficients for the model were estimated using logistic regression. We used this structure, following the resource selection function literature (Manly et al., 1993; Boyce et al., 2002), as we were sampling our GIS for zeros (psuedo-absences) and hence not directly measuring absences. A global mortality distribution model representing all recorded mortalities was developed along with specific models for significant demographic status, season, and mortality type classes identified as significant in the previous section. Model significance was determined using those methods described previously, while standard error estimates and associated coefficient significance were calculated using a 499 bootstrap sample. Bootstrap estimates did not require any assumptions beyond the sample being representative of the underlying process and therefore were considered more robust (Manly, 1991).

To validate our models, we partitioned mortality data prior to model building into a model-training and model-testing data set. Model-training data and random (psuedo-absences) locations were used to develop model coefficients, while model-testing data were used for within sample independent validation. We approximated the ratio of training and testing data using Huberty's rule of thumb (Huberty, 1994) where 80% of the randomly chosen data were used for training and 20% were used for testing. Using the test data, we examined the predictive capacity of the model (validation) by comparing model predictions to the observed number of withheld mortalities (Boyce et al., 2002). Mortalities were summed within five ranked bins representing low to high mortality predictions. Division of the five bins was based on a standard deviation classification of model predictions using the reclassification function in Spatial Analyst (ArcGIS 8.2). We used a Somer's D statistic, with jackknifed standard errors, to compare the number of withheld testing data mortalities within standardized bins (based on the area of that bin) and the ranking of that bin. A Somer's D test can be interpreted in a similar manner to that of a Spearman rank correlation, where concordance ranges from –1 to 1. A significant positive relationship would be interpreted as a model that was predictive and characterized by successively greater number of mortalities within increasing bin ranks (i.e., more mortalities were occurring in higher risk of mortality sites standardized for area).

3.3.4. Radiotelemetry versus mortality locations – the mortality risk model

Because the previous comparison between random and mortality locations does not consider the conditional nature of the mortality process (i.e., bears can only be killed where they are present, not necessarily all [random] locations), we also used logistic regression to contrast the location of grizzly bear mortalities with sites used by grizzly bears. We determined grizzly bear use by collecting 3089 VHF radiotelemetry locations from 60 sub-adult and adult (35 female: 25 male) grizzly bears between 1994 and 2001. Similar methods were used for developing a mortality risk model as those in the previous section (Eq. (2)) with the distinction being that radiotelemetry (0), not random locations, were contrasted with mortality (1) locations. In the context of survival modelling (Cox and Oakes, 1984), our radiotelemetry locations would closely match that of exposure, as these locations were sites where the animal was known to have occurred and survived. Radiotelemetry locations were considered to be accurate within 150 m of the estimated location (Gibeau, 2000). For this analysis, all mortalities located outside the 100% minimum convex polygon (MCP) home range of individual radio-collared grizzly bears were excluded. The merged MCP home ranges therefore represented our spatial extent for this analysis. Coefficients from this analysis were compared with the mortality distribution model (random

versus mortality locations) to identify potential differences. We interpreted coefficients from the mortality risk model to represent those areas where grizzly bears are likely to die given that they selected particular habitats and resources (a form of conditional probability not satisfied with a comparison of random locations). Finally, we compared the ranked predictions of mortality distribution model with the mortality risk model using a weighted Kappa (K_w) statistic (Monserud and Leemans, 1992; Næsset, 1996). The weighted Kappa statistic was used instead of traditional Kappa given that categories of risk were ordered. We consider Kappa values greater than 0.75 to indicate very good to excellent agreement (1.0 is perfect), while values between 0.4 and 0.75 indicate fair to good agreement, and finally values less than 0.4 to indicate poor agreement (Landis and Koch, 1977).

4. Results

4.1. Spatial densities of grizzly bear mortalities

Regardless of the scale examined, grizzly bear mortalities were concentrated within three regions of the Alberta study area; (1) Lake Louise; (2) Banff town site; and (3) Alberta Provincial lands near the Red Deer River northwest of Calgary (Fig. 2). For the 900- and 1405-km²-scales, mortality densities within moving

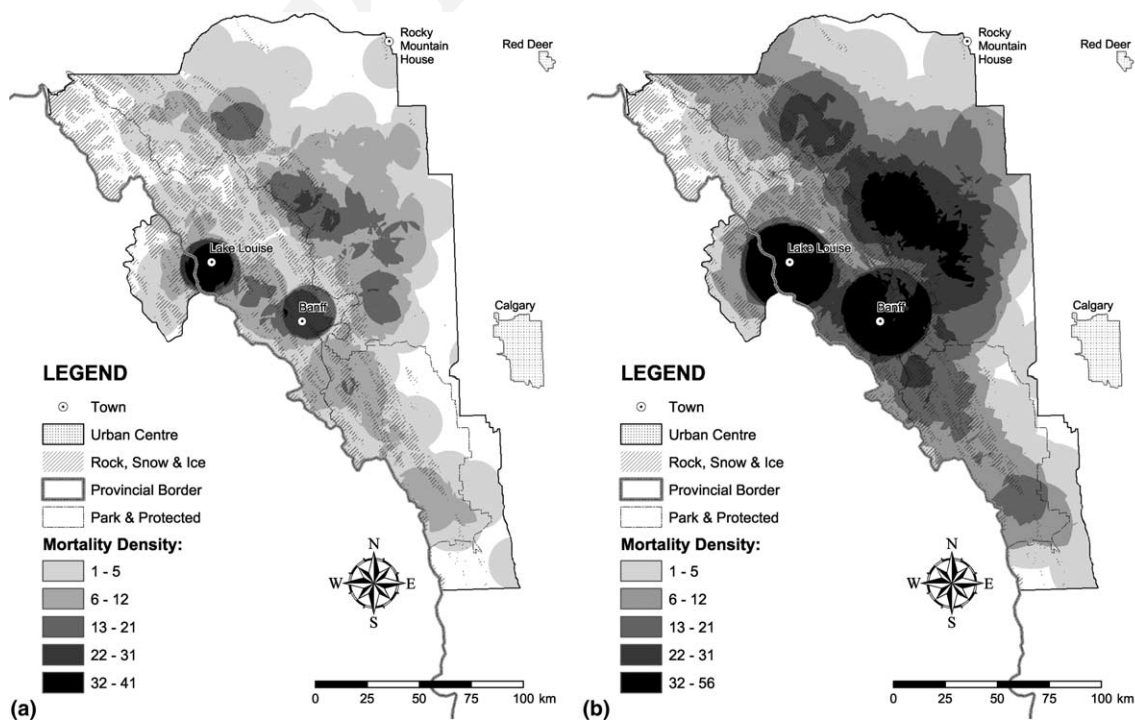


Fig. 2. Distribution and concentration (density of recorded mortalities) of grizzly bear mortalities within the study area at two scales relating to the multi-annual 95% fixed kernel home ranges for female (a, 520-km²) and male (b, 1405-km²) grizzly bears. Note the differences between scales and the high concentration of mortalities near Banff and Lake Louise town sites as well as the east slopes northwest of Calgary. A third scale relating to the lifetime home range of a Yellowstone grizzly bear (900-km²) is not shown but is intermediate between the scales depicted.

Table 1

Percent composition of qualitatively defined secure (0 recorded mortalities), secure but non-habitat (rock, snow, ice, water), and high mortality density sites (>31 mortality events) for the Central Rockies ecosystem of Canada

Variable	Percent of landscape		
	520-km ²	900-km ²	1405-km ²
Secure	23.9	13.9	7.2
Secure, non-habitat	21.8	23.2	32.0
High mortality density	1.4	3.8	13.2

Mortality density estimates were based on moving windows of three scales, the first relating to local female home range sizes (520-km²), the second Yellowstone lifetime home range sizes (900-km²), and third local male home range sizes (1405-km²).

windows exceeded 31 mortalities for the above three identified areas, equivalent to ≥ 1 mortality event/year and qualitatively considered a high mortality zone. At the 520-km²-scale, only Lake Louise stood out in having more than 31 mortality events, although a very small area west of Banff also showed high mortality. Total area occupied in a high mortality zones ranged from 1.4% at the 520-km²-scale to 13.2% for the 1405-km²-scale (Table 1). In contrast, the total area considered secure from human-caused mortalities (no recorded mortality events) ranged from 7.2% for the 1405-km²-scale to 23.9% for the 520-km²-scale (Table 1). However, 22–32% of secure habitat was in areas of non-habitat (Fig. 2, Table 1) suggesting an even more restricted extent for security over the past 32-years.

4.2. Mortality differences among demographic status, season, and mortality type

The landscape features at mortality locations for male and female grizzly bears were not differentiated by logistic regression ($\chi^2 = 8.38$, $p = 0.497$, d.f. = 9) (Table 2). Conversely, we found strong differences between sub-adult males and other sex-ages. The sub-adult male model was significant overall ($\chi^2 = 27.77$, $p = 0.001$, d.f. = 9) with distance to access feature and edge variables significant. Generally, sub-adult male mortalities were further from edges than other sex-age classes (Table 2). In addition, sub-adult male mortalities were more likely to be further from human access features than adult, young, and sub-adult female mortalities.

We did not find any temporal effects associated with berry season (August 1 to October 31), as the overall model was non-significant ($\chi^2 = 12.04$, $p = 0.211$, d.f. = 9). Finally, comparisons of legal harvest with other human-caused mortalities showed strong spatial environmental differences for mortality locations with a significant overall model ($\chi^2 = 23.30$, $p = 0.006$, d.f. = 9) and significant variables for distance to habitat edge and access features. Legal harvest locations occurred further from edges and access features compared with other

Table 2
Estimated coefficients (Coeff.) for GIS environmental predictor variables used to estimate if any spatial mortality differences existed among specific demographic status, sex-age, season, or mortality class when compared with other mortalities (e.g., berry season compared with non-berry season)

Variable	Female			Sub-adult male			Berry season			Legal harvest		
	Coeff.	S.E.	p	Coeff.	S.E.	p	Coeff.	S.E.	p	Coeff.	S.E.	p
<i>Land cover type</i>												
Deciduous forest	0.109	0.463	0.814	-0.906	0.628	0.149	-0.046	0.455	0.919	0.075	0.590	0.899
Grassland	-0.021	0.461	0.964	-0.096	0.561	0.864	0.358	0.470	0.446	-0.341	0.577	0.555
Non-vegetated	0.636	0.745	0.393	- ^a			0.726	0.749	0.332	-0.846	1.118	0.449
Shrub	0.010	0.356	0.978	-0.338	0.428	0.430	0.355	0.375	0.344	0.302	0.467	0.518
Greenness	0.010	0.073	0.891	0.005	0.090	0.959	0.048	0.074	0.511	-0.170	0.088	0.052
Distance to edge	-4.580	5.424	0.398	11.700	5.620	0.037	-9.293	5.749	0.106	11.977	6.119	0.050
Distance to water	-0.266	0.673	0.693	-1.732	1.040	0.096	0.741	0.671	0.270	-0.841	0.946	0.374
Distance to access	-0.736	0.370	0.047	0.942	0.353	0.008	-0.520	0.355	0.143	0.780	0.359	0.030
Terrain variability	3.251	3.464	0.348	-5.222	4.520	0.248	0.785	3.457	0.820	3.532	4.100	0.389
Constant	-0.317	0.750	0.672	-0.824	0.922	0.371	-0.952	0.773	0.218	0.641	0.947	0.498

Conifer forest was used as the reference category (indicator contrast) for comparisons with other land cover classes

^a Estimated coefficient convergence failed due to perfect classification (no sub-adult male mortalities recorded in non-vegetated areas).

mortalities, interpreted to mean that hunters must go further from a road to harvest bears and in other contexts, such as problem bears, human-caused mortality occurs nearer to roads.

4.3. Random versus mortality locations – mortality distribution models

Irrespective of differences in demographic status, season, and mortality type, the global mortality distribution model significantly ($\chi^2 = 144.91$, $p < 0.001$, d.f. = 9) described grizzly bear mortalities within the studied portion of the CRE. Mortalities were positively associated with access, water, and edge features (i.e., negative coefficients for distance to feature), while negatively associated with terrain ruggedness and greenness indices (Table 3). Only the shrub land cover class proved to be significantly different from that of conifer forests, having higher mortality ranks. Spatial model predictions for the global model showed strong patterns of high mortality along the eastern slopes of the Rockies and human accessible areas within the Parks (Fig. 3). Using the independent withheld testing data (validation) we found our global mortality distribution model to be predictive overall with scaled bins of relative mortality ranks relating to the number of mortality locations falling within those bins ($D = 1.0$, $p < 0.001$; Fig. 4).

Models describing sub-adult male mortalities were significant ($\chi^2 = 93.19$, $p < 0.001$, d.f. = 9) showing an association with water, low greenness sites, less rugged terrain, and in shrub habitats (Table 3). In contrast, the distance variables for edge and access features, although negative (more likely to be near that feature), were not significant. For the other sex-age class, however, mortalities were strongly related to edges and access features, with a significant model overall ($\chi^2 = 79.43$, $p < 0.001$, d.f. = 9). Similar to sub-adult males, mortalities for the other sex-age class were in low greenness sites and in less rugged terrain. Not only were other sex-age class mortalities more likely to occur in shrub habitats, but also in grassland areas (Table 3). In comparison to other sex-age classes, sub-adult male mortalities tended to occur further from edges and access features, nearer to water, and in less rugged terrain.

Models describing legal harvest mortalities were significant overall ($\chi^2 = 48.11$, $p < 0.001$, d.f. = 9), showing a strong association with water and less rugged terrain. Hunters were apparently successful in focusing their attention to streamside habitats, where animals are typically concentrated during the spring hunting season. There were non-significant, but consistent negative (nearer to features as for previous groups) relationships for access, edges, and greenness. For land cover types, only the shrub category was significantly different from

Table 3
Estimated coefficients (Coeff.) for models describing the relative probability of grizzly bear mortality within the Central Rockies ecosystem of Canada by contrasting mortalities with random locations

Variable	Global model (all)			Sub-adult male			Other sex-age			Legal harvest			Non-harvest/other		
	Coeff.	S.E.	p	Coeff.	S.E.	p	Coeff.	S.E.	p	Coeff.	S.E.	p	Coeff.	S.E.	p
<i>Land cover type</i>															
Deciduous forest	0.405	0.264	0.125	-0.098	0.539	0.856	0.415	0.359	0.248	0.398	0.487	0.413	0.536	0.493	0.277
Grassland	0.212	0.233	0.363	0.108	0.416	0.795	0.503	0.339	0.137	-0.138	0.530	0.795	0.931	0.361	0.010
Non-vegetated	-0.158	0.414	0.702	-0.629	3.108	0.840	0.592	0.487	0.224	-1.242	4.633	0.789	-0.140	4.622	0.976
Shrub	0.813	0.205	<0.001	0.784	0.318	0.014	1.023	0.276	<0.001	0.753	0.368	0.040	1.034	0.345	0.003
Greenness	-0.133	0.041	0.001	-0.144	0.076	0.057	-0.152	0.054	0.005	-0.146	0.076	0.057	-0.074	0.066	0.267
Distance to edge	-7.792	2.270	0.001	-6.005	3.032	0.048	-11.738	3.608	0.001	-3.251	2.545	0.201	-11.076	4.033	0.006
Distance to water	-2.274	0.549	<0.001	-3.524	1.291	0.006	-1.490	0.634	0.019	-3.499	1.252	0.005	-2.141	1.032	0.038
Distance to access	-1.630	0.474	0.001	-0.632	0.588	0.282	-2.901	0.910	0.001	-0.322	0.409	0.431	-2.652	0.889	0.003
Terrain variability	-8.090	1.599	<0.001	-10.598	2.533	<0.001	-6.740	2.048	0.001	-6.596	2.504	0.008	-4.086	2.471	0.098

Standard errors (S.E.) and inferences were based on a 499-sample bootstrap estimate. Conifer forest was used as the reference category (indicator contrast) for comparisons with other land cover classes.

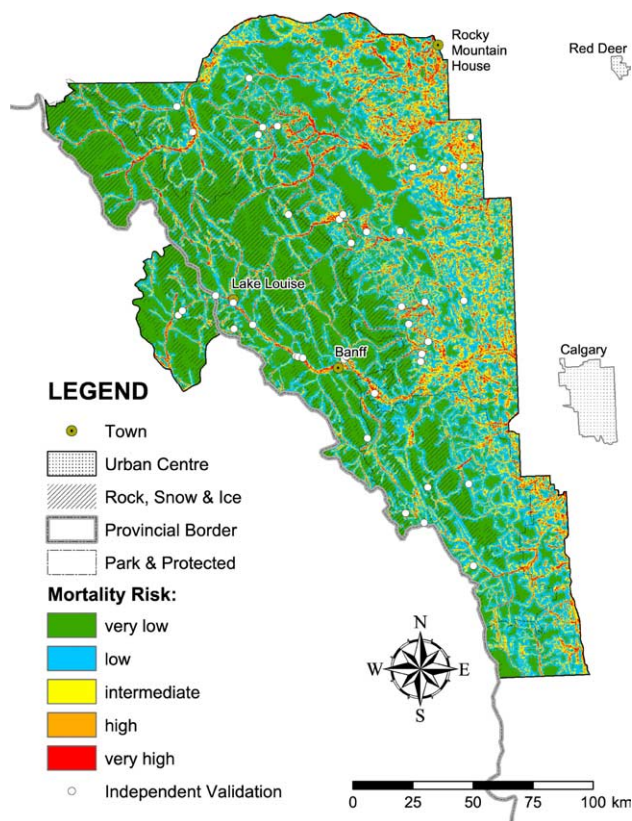


Fig. 3. The distribution of mortality ranks from very low to very high based on the global mortality distribution (random versus mortality locations) model in the Central Rockies ecosystem of Canada.

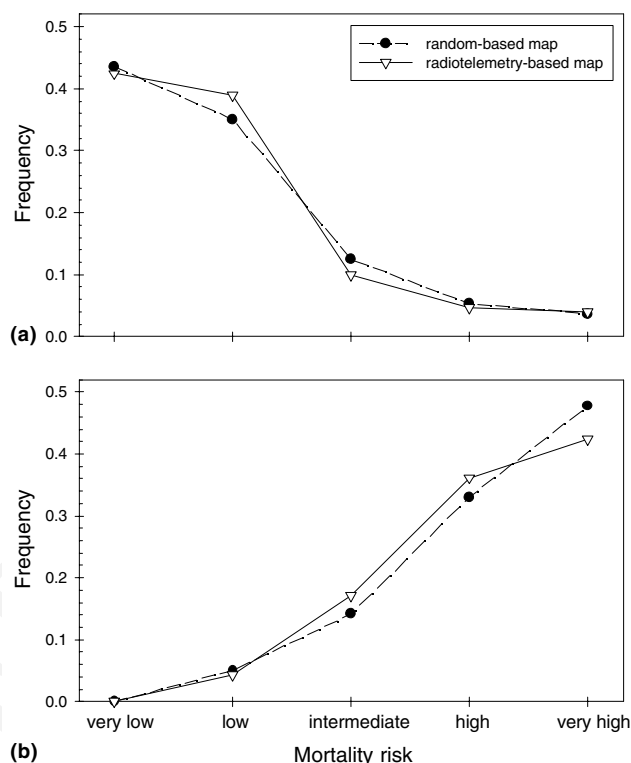


Fig. 4. Percent composition of very low to very high mortality risk pixels in the Central Rockies ecosystem of Canada based on the mortality distribution (random-based map) and the mortality risk (radiotelemetry-based map) models (a). Area-adjusted frequency of withheld (testing data) mortality validations ($n = 45$) falling within very low- to very high-mortality risk bins (b). Although only a small fraction of mortality pixels are in high and very high bins (a), the majority of mortalities (per area) are occurring in these sites (b).

590 that of closed conifer stands (Table 3). Non-harvest
 591 mortalities, on the other hand, were not only more likely
 592 to occur in shrub habitats, but also in grasslands with a
 593 significant model overall ($\chi^2 = 57.07$, $p < 0.001$,
 594 d.f. = 9). Distance to edge and access also were impor-
 595 tant indicators of non-harvest mortalities. Both were
 596 strongly negative, suggesting that vegetation edges and
 597 human-accessible areas were more dangerous for non-
 598 harvested grizzly bears. Greenness, distance to water,
 599 and terrain variability were non significant, but were still
 600 negative, suggesting a weak association. In contrast to
 601 non-harvest mortalities, legal harvests mortalities ten-
 602 ded to occur further from access and edge features,
 603 nearer to water, less likely in grasslands, and finally, in
 604 less rugged terrain.

605 4.4. Radiotelemetry versus mortality locations – the 606 mortality risk model

607 The mortality risk model, describing radiotelemetry
 608 versus mortality locations using GIS predictor variables,
 609 was significant overall ($\chi^2 = 170.49$, $p < 0.001$, d.f. = 9).
 610 Mortality locations occurred in deciduous forest and
 611 shrub land cover classes more so than closed conifer
 612 stands (reference). Also, grizzly bear mortalities were
 613 more likely to occur nearer to edge, access, and water

variables (Table 4). Finally, grizzly bear mortalities were
 significantly related to areas of low greenness and min-
 imal terrain ruggedness. Overall predictions of mortality
 classes and validations of withheld mortalities within
 these classes were similar for the mortality risk and
 mortality distribution models (Fig. 4). Coefficient cov-
 erage between the random-versus-mortality and the ra-
 diotelemetry-versus-mortality models failed to reveal
 large differences, although stronger associations of
 mortality for less rugged terrain, near edges, and within
 the deciduous land cover class was evident for the
 mortality risk model (radiotelemetry versus mortality
 locations). Furthermore, a weighted Kappa statistic
 ($K_w = 0.78$) suggests very good to excellent agreement in
 the spatial predictions of mortality sites by the mortality
 distribution and mortality risk maps. Using the inde-
 pendent withheld testing data (validation) we found our
 global mortality risk model to be predictive overall with
 scaled bins of mortality risk relating to the number of
 mortality locations falling within those bins ($D = 1.0$,
 $p < 0.001$; Fig. 4). The similarities with our mortality
 distribution model (random versus mortality locations)
 suggest that the random versus mortality locations were
 not overly tied up in habitat selection, but instead re-

Table 4

Comparison of the mortality distribution (random versus mortality locations) and mortality risk (radiotelemetry versus mortality locations) with bootstrapped standard errors and significance

Variable	Mortality distribution model			Mortality risk model		
	Coeff.	S.E.	<i>p</i>	Coeff.	S.E.	<i>p</i>
<i>Land cover type</i>						
Deciduous forest	0.405	0.264	0.125	1.199	0.322	<0.001
Grassland	0.212	0.233	0.363	−0.034	0.378	0.928
Non-vegetated	−0.158	0.413	0.702	0.331	0.618	0.593
Shrub	0.813	0.205	<0.001	0.832	0.235	<0.001
Greenness	−0.133	0.041	0.001	−0.182	0.056	0.001
Distance to edge	−7.792	2.27	0.001	−12.969	4.895	0.008
Distance to water	−2.274	0.549	<0.001	−1.146	0.605	0.058
Distance to access	−1.630	0.474	0.001	−2.003	0.990	0.043
Terrain variability	−8.090	1.599	<0.001	−14.729	2.146	<0.001

lated to those processes influencing human-caused grizzly bear mortality.

5. Discussion

Grizzly bear mortalities were concentrated in three regions of the study area: (1) Lake Louise; (2) Banff town site; and (3) Alberta Provincial lands near the Red Deer River (Benn, 1998). Unlike Lake Louise and Banff, a large proportion of human-caused mortalities in the Red Deer River basin were caused by legal spring harvests. For two scales (900- and 1405-km²), the number of mortalities within home-range-sized moving windows exceeded or equalled the number of years examined (≥ 1 mortality/year) for these three regions suggesting very high mortality rates. Temporal variation in mortalities over the past three decades have, however, been evident for different regions, with some areas like the Banff town site exhibiting reduced rates of mortality in the past number of years (Benn, 1998; Benn and Herrero, 2002). Secure areas varied from 7.2% to 23.9%, although large proportions of these areas were considered to be non-habitat.

Comparisons of demographic status, season, and mortality type revealed spatial discriminations in mortalities for sub-adult male/non-sub-adult male and legal hunting/non-legal hunting locations, while sex and season differences were similar. We found no spatial differences in mortality for season (berry versus non-berry season), despite reported differences in total number of mortalities (Benn and Herrero, 2002). Benn and Herrero (2002) found that a high proportion of mortalities occurred in the berry season when bears were most likely to forage at low elevation sites for russet buffaloberry, *Shepherdia canadensis*, fruits. Although grizzly bears were more likely to be 'killed' during the hyperphagic berry period when they were accessing habitats near humans (e.g., low elevation sites), these sites were spatially similar to those of other

mortalities occurring in the non-berry seasons. This suggests that the spatial locations of mortality sinks (*sensu* Knight et al., 1988) were consistent and only the number (rate) of mortalities varied by season. For the sub-adult male and non-sub-adult male comparison, we found that sub-adult males tended to be 'killed' further from access and edge features when compared with non-sub-adult males, although variation in distance to access for sub-adults was high suggesting that animals were 'killed' both near and away from access features. Although we expected sub-adults to be further from edges through aggressive displacement of by adult males (McLellan and Shackleton, 1988), we were surprised to find sub-adult male mortalities further from access features where you would expect most mortality events to occur regardless of sex-age class. Perhaps, sub-adult males were simply more broadly distributed across the landscape and this was reflected in mortality locations. Finally, the legal harvest versus non-legal harvest comparison revealed that legal harvests were further from edges and access features. This suggests that during the hunting season grizzly bears are further from edges and access or hunters were accessing more remote areas during the hunt.

For the global data set, the random-based mortality distribution model and the radiotelemetry-based mortality risk model revealed similar mortality patterns that were largely consistent with the literature and expected distribution of bears. Grizzly bear mortalities were positively associated with access, water, and edge features (e.g., nearer to those features or a negative coefficient). Previous research in the region has shown that bears select edge habitats and streamside areas (Nielsen et al., 2002; Theberge, 2002), but we also suspect that humans are more likely to be in these sites as well, thereby increasing the frequency of contact between bears and humans (Mattson and Merrill, 1996a, 1996b). Distance to access features, on the other hand, is more likely to describe the distribution of humans in space. Where bear habitat co-occurs with

human access, however, interactions between bears and humans will escalate thereby increasing risk of human-caused mortality to bears. Although previous research in the area has shown positive associations between grizzly bear occurrence and both terrain ruggedness and the vegetation index greenness (Mace et al., 1999; Nielsen et al., 2002; Stevens, 2002; Theberge, 2002), we found negative associations for models describing mortality sites. Our models did not consider, however, the overall spatial pattern or patchiness of greenness like that of Stevens (2002), and thus may reflect the strong association of mortalities with edges, stream side areas, and roads, where pixel values for greenness are likely to be low. Likewise, for terrain ruggedness, we suspect that terrain patterns in mortalities is likely to be related more with human distribution than grizzly bear distribution as humans are less likely to venture into more rugged terrain, at least when compared to grizzly bears. Finally, for land-cover type classes, shrub (including avalanche) habitats were consistently more likely to have mortalities than the reference category closed conifer stands. We feel this reflects the strong concentration of bears within shrub and avalanche areas (Theberge, 2002).

Overall, global models describing the distribution of mortality risk were predictive and significant based on the occurrence of independent grizzly bear mortalities withheld for model validation. This suggests that mortalities were well described and predictable using readily available terrain, human, and vegetation GIS data. This is further supported by the methods and results observed by Johnson et al. (in press) in the spatial describe grizzly bear survival in the Greater Yellowstone ecosystem. Although our models were not based on the more powerful Cox regression methods (Cox and Oakes, 1984) for survival (1-mortality), as we did not track exposure and ultimately death for individual animals, our mortality risk model would likely closely match ranks from a survival model. Baseline survival functions from other studies might be used to scale our predictions. The fact that Johnson et al.'s (in press) survival model for Yellowstone and our mortality risk model for the CRE qualitatively provide similar responses to similar types of GIS data suggest that information from other areas can readily be used to describe areas of grizzly bear mortality risk, as human behaviour ultimately causing grizzly bear deaths appears to be consistent.

6. Management implications

Conservation models describing grizzly bear mortality locations in the CRE of Canada are needed for to management and conservation planning. As would be expected, landscape attributes relating to human use, such as roads, trails, and terrain, correlated well with the

locations of human-caused grizzly bear mortalities. Spatial mortality models, as those presented in this paper, can be used for management of humans in grizzly bear territories and the identification of potential restoration (road access control or deactivation) sites. Moreover, incorporation of risk models with existing animal occurrence models (e.g., Nielsen et al., 2002, 2003) may prove useful for assessments of population viability (Boyce and McDonald, 1999) and attractive sink dynamics (Delibes et al., 2001; Naves et al., 2003). We suggest that risk models be integrated with habitat models for identifying key habitat sinks and secure areas for active management and protection respectively.

Management and mitigation of potential habitat sinks may be necessary, at minimum during essential activities such as the hyperphagic berry period (August to October) or the spring limited entry bear hunt when the majority of animals are at high risk and killed by humans (Benn and Herrero, 2002). Concurrently, education programmes for the public and hunters may be necessary to reduce bear-human conflicts (Schirokauer and Boyd, 1998). Finally, management policies regarding problem wildlife may need further modification and/or examination of population impacts. Numerous animals were lost to the CRE by relocation and/or problem wildlife mortalities (Benn, 1998). The number of management actions a grizzly bear received increased substantially the risk of mortality (Boyce et al., 2001; Johnson et al., in press). This suggests that behavioural patterns exhibited by some bears may place them at greater risk and those management policies and actions for these animals were not successful in ultimately reducing mortality. Managers should consider alternatives to animal relocation, such as aversive conditioning, while striving to minimize habituated and problem animals from first developing. Even with well-intended management plans, maintenance of viable grizzly bear populations in southern Canada is increasingly difficult given the rapid growth in human population, land use pressure, and recreation within grizzly bear range (McLellan, 1998). Addressing access management for grizzly bear populations, now being considered for threatened status by the Alberta government, may be necessary to stem localized mortality sinks. Implementation of human recreation and waste management policies in the National Parks has reduced local human-bear conflicts (Benn, 1998). We found that relatively little of the landscape was secure from human-caused mortality for grizzly bears. This would be most directly remedied by decreasing access.

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